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Personality and the collective: bold homing pigeons occupy higher leadership ranks in flocks

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While collective movement is ecologically widespread and conveys numerous benefits on individuals, it also poses a coordination problem: who controls the group's movements? The role that animal 'personalities' play in this question has recently become a focus of research interest. Although many animal groups have distributed leadership (i.e. multiple individuals influence collective decisions), studies linking personality and leadership have focused predominantly on the group's single most influential individual. In this study, we investigate the relationship between personality and the influence of multiple leaders on collective movement using homing pigeons, *Columba livia*, a species known to display complex multilevel leadership hierarchies during flock flights. Our results show that more exploratory (i.e. 'bold') birds are more likely to occupy higher ranks in the leadership hierarchy and thus have more influence on the direction of collective movement than less exploratory (i.e. 'shy') birds during both free flights around their lofts and homing flights from a distant site. Our data also show that bold pigeons fly faster than shy birds during solo flights. We discuss our results in light of theories about the evolution of personality, with specific reference to the adaptive value of heterogeneity in animal groups.

This article is part of the theme issue 'Collective movement ecology'.

1. Introduction

Moving as a group has numerous benefits for social animals: among others, it dilutes predation threat, facilitates distributed sensing of potential food sources and allows the sharing of information during navigation [1]. However, collective movement can also pose a coordination problem: when individuals have conflicting preferences or interests, how can they reconcile these differences? In groups where input is not combined with equal weight from all members (i.e. as it is in equally shared decisions; [2]), certain individuals can emerge to exert a disproportionate influence on collective decision-making [3], including on the direction of collective travel [4–9]. Past studies have identified a variety of traits, such as experience, sex, age and social dominance, that affect individuals' propensity to assume leadership [1,4,8,10,11]. For example, older individuals have stronger influence on collective decisions in African elephants [11], and socially dominant grey wolves are more likely to initiate pack activities than subordinates [12].

Recently, the effects of 'personality' traits on leadership have become a focus of intense research interest. Personality denotes a spectrum of individual behavioural differences that are consistent over time and across different contexts [13,14] (but see also [15]). The most commonly studied personality trait is the shy–bold spectrum of behaviour [13]. Bold individuals are those who show a greater propensity to explore, to move away from safe locations and from

other individuals, and to investigate novel sensory cues. It has been demonstrated that individuals with certain personality traits contribute differently to collective movement in various species, including in fish, birds and sheep [16–22], where bold individuals exhibit an increased tendency to become leaders.

Studies linking personality and leadership have, however, focused predominantly on one position—the front—effectively categorizing all individuals in the group according to a single dichotomy: leader versus followers. That is, an individual who first departs when the group moves categorized as a leader, while all others who come after are categorized as followers [19,23,24]. This is partially because collective movements are frequently depicted as originating from one individual (the leader, or decision-maker) initiating movement. We argue that this is an oversimplification that limits our understanding of the potentially delicate interaction between personality and leadership. That leadership can, in fact, be distributed among several group members during collective movement has been demonstrated in various taxa (see [25] for a review). The extent to which individual personality traits influence ranks in such more complex, distributed leadership networks remains to be elucidated.

In this study, we used flocks of homing pigeons, *Columba livia*, to investigate the relationship between personality and influence on collective movement. Pigeons spontaneously engage in group flights around their home loft as well as during homing from distant sites, where conflicts over route choice may arise due to inter-individual differences in route preferences [26]. Past research has identified determinants of leadership in pairs of pigeons navigating together, such as navigational experience [27] and route fidelity [28]. However, even in this simple paired scenario, one individual acts as a leader for only parts of the homing flight: at times during the same flight, the two birds may contribute equally, or they may swap leadership for different segments of the journey [26]. In larger flocks, such pairwise interactions lead to the emergence of a more subtle organizational principle than a single leader with multiple followers. Instead, collective decision-making is hierarchically organized, where all or most individuals within the flock contribute to some extent to the flock's decisions, but they do so with consistently different weights [29].

Which factors correlate with leadership in pigeon flocks has been investigated in a series of experiments targeted at observing and/or manipulating individual variation in specific traits. For example, a recent study showed that social dominance had no effect on birds' ranks in the leadership hierarchy [30]. Furthermore, additional navigational experience given to mid-ranked individuals did not lead to an increase in their leadership ranks [31]. Another study later showed that pigeons with more navigational experience tended to occupy the top hierarchical rank; however, experience did not determine the order in which birds assumed the other ranks (i.e. birds with more experience did not necessarily occupy the top half of the leadership hierarchy, even though multilevel leadership hierarchies continued to be observed) [32]. Finally, with other factors being equal, pigeons that flew faster in an asocial context tended to lead collective movement [33], suggesting that leadership may emerge as a consequence of inherent heterogeneity in individual flight characteristics. In short, so far only flight speed has been shown reliably to correlate with the ordering of leadership ranks into flocks.

Beyond the factors already tested, other candidates generating inter-individual heterogeneity remain. In this study, we therefore investigate personality: not only has this factor not been tested in navigating pigeon flocks, but we do not know what role the shy–bold spectrum plays, if any, in structuring the complex interplay between individual variation (in, for example, flight speed) and leadership hierarchies.

Our experiment consists of three phases. We first perform individual behavioural assays of exploratory behaviour, considered one of the major manifestations of personality [34,35]. We then release subjects individually to measure their solo flight performance in terms of speed, route efficiency and route fidelity, seeking individual characteristics that may moderate any observed relationship between leadership and personality. Finally, we test whether personality type is predictive of an individual's rank in the leadership hierarchy during both homing flights from distant sites and free flights around the birds' lofts.

2. Material and methods

(a) Subjects

We used 96 homing pigeons (45 and 51 birds for the first group (used in Experiments 1–3) and the second group (used in Experiment 4), respectively; see below for details of experiments), *C. livia*, bred at the Oxford University Field Station, Wytham, UK (51°46'58.34" N, 1°19'02.40" W). They were kept in a social group of approximately 140 pigeons inside two lofts and had free access to the outside. Subjects were between 1 and 7 years of age (mean = 3.5 years) and weighed between 380 and 494 g (mean = 419 g). They had experience of homing from four training release sites (electronic supplementary material, table S1) in solo flights and as a flock three months prior to the present experiments. Birds older than 2 years had participated in homing experiments in previous years; however, they had never been released from any sites within 3 km of those used in the current study. None of the subjects had ever participated in any indoor/laboratory experiments; the exploratory behaviour test (see below) was equally novel to all birds.

Subjects were equipped with either an elastic harness 'backpack' [29] or a soft plastic pouch velcroed to the back [32], into which a GPS device (see below) was placed during each release. Between releases, subjects carried a Plasticine dummy weight (15 g) inside the backpack/pouch.

(b) Experimental procedures

(i) Exploratory behaviour test

To assess birds' personality on the shy–bold spectrum, we measured how quickly birds exited a 'shelter' into open space. The shelter was a cardboard box (34 cm × 27 cm × 27 cm), and the open space a narrow, 27 cm wide passage in which birds could walk but not fly (figure 1). A bowl of food (multigrain mixture) was placed at the end of the passage furthest from the box. At the beginning of each trial, a pigeon was placed in the box and an opaque cover was placed in front to keep it inside. After 3 min, the experimenter slowly removed the cover and stood approximately 1 m behind the box, outside of the subject's visual field. Once the subject had left the box completely (i.e. its whole body was outside of the box), the experimenter terminated the trial by catching the pigeon before it reached the food to make sure that this exploratory behaviour was not reinforced. The pigeon was then immediately returned to the loft. If the pigeon did not exit the box within 10 min, the experiment was terminated using the same procedure.

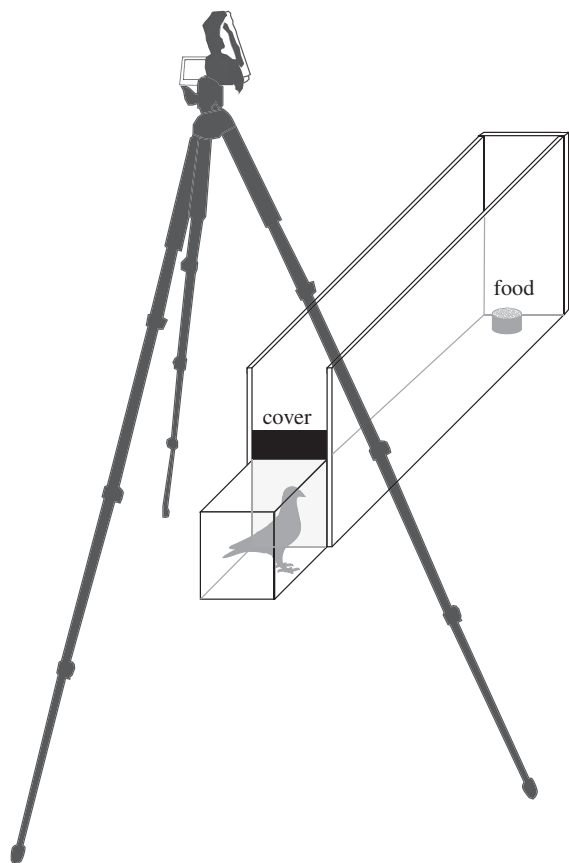


Figure 1. Experimental arena for measuring exploratory behaviour. A subject initially held in the box at one end of the passage is released by removing the plastic door cover. Food is available at the other end of the passage. The length of time it takes the subject to fully leave the box is determined from video footage recorded by a video camera mounted above the apparatus.

Each bird in the first group was tested twice; those in the second group were tested three times. The second test took place 1–2 days after the first, and the third three months later. Each test was filmed from above using a tripod-mounted video camera (HC-V520, Panasonic, Japan).

In each test, we designated a bird as ‘bold’ if it left the box sooner than the median latency, and as ‘shy’ if it left later than the median or if it did not exit at all. The median was 309.5 s across the two groups. We treated personality as a binary variable, rather than a continuous variable, because the 600-s trial cut-off meant that for birds at the shy end of the spectrum we encountered a ceiling effect, rather than recording measurements of actual latency. Similar to our approach, personality type is commonly treated as a binary variable in animal behaviour research [13,35–37]. In the following experiments, we used only the birds who showed consistent personality (i.e. same personality types across all the behavioural tests).

(ii) Experiment 1: flight characteristics during solo homing

We first tested if bold and shy birds differ in their flight characteristics during solo homing. Based on the results of the exploratory behaviour tests, we selected the 12 boldest (i.e. those with the 12 shortest mean latencies) and 12 shyest (those with the 12 longest mean latencies) birds out of 45 and did not use the 21 birds in the middle for this experiment. We then released them 13 times individually from the same site (Church Hanborough: 51°48′44.3″ N, 1°22′38.3″ W; distance to home: 5.2 km, direction to home: 128°) with 5 Hz GPS loggers

(15 g; BT-Q1300ST, Qstarz, Taiwan). One of the shy birds did not return on its first release, leaving a sample size of 11 shy birds. Up to four releases were conducted per day, with a minimum of 1 h between releases, in dry weather and at wind speeds less than 10 m s⁻¹. All the releases in the following experiments were conducted using the same methods and under similar weather conditions (May to August).

(iii) Experiment 2: leadership hierarchies during homing flights

We next measured if boldness is related to leadership during flock homing flights. Using the same birds as those in Experiment 1, we constructed three flocks, each composed of four bold pigeons and four shy pigeons (eight pigeons per flock) except one, which had four bold pigeons and three shy pigeons (seven pigeons per flock). We tested the relationship between boldness and leadership by releasing these flocks from the same site as that used in Experiment 1 four times and reconstructing their leadership hierarchies from GPS data.

(iv) Experiment 3: leadership hierarchies during homing flights from a novel site

Experiment 2 showed that bold birds occupy higher ranks in leadership hierarchies during homing flights from a site where they had previously been released solo (see Results for details). We hypothesized that this pattern might have been caused by birds’ experience during the solo flights: for example, if bold individuals naturally learn routes better than shy birds during solo flights, this difference in knowledge may allow bold individuals to emerge as leaders during flock flights (see [27] for evidence of a related, experience-based effect in pairs). To eliminate this possibility, we released the flocks of Experiment 2 from a novel site (Noke: 51°48′40.9″ N, 1°13′12.0″ W; distance to home: 7.3 km, direction to home: 244°) six times. Although the site would only have been truly novel to the subjects on the first of these releases, because pigeons typically take eight to 10 releases to establish their routes (see [38] for a review), we considered them to still possess relatively low landscape familiarity over the first six releases. We then again assessed the relationship between birds’ leadership hierarchical ranks and their boldness. Because some of the birds used in Experiment 2 were no longer available (some were being used in another experiment, and one had died), the flock sizes became smaller: two flocks were composed of six pigeons (three bold and three shy) and one was composed of seven pigeons (four bold and three shy).

(v) Experiment 4: leadership hierarchies during free flights around lofts

A previous study showed that pigeon leadership hierarchies can be observed not only during homing flights but also during free ‘circling’ flights in the vicinity of the loft [29]. Thus, in this study, we tested if boldness is also related to leadership during such free flock flights by releasing flocks immediately next to their lofts. We measured exploratory behaviour in an additional 51 birds and selected the 15 boldest and 15 shyest individuals. The remaining 14 birds were not used. Using these selected birds, we constructed three flocks, each composed of five bold pigeons and five shy pigeons (10 pigeons per flock). We released each flock 12 times. Flights lasted an average of 365 s (range: 21–964 s), ending when the last bird of a given flock landed back on the loft.

(vi) Analysis

Individual personality. We tested for repeatability in the personality measure over successive assays for each individual. Our measure of repeatability was the probability that the bird exhibited the same personality type (which we had measured on the basis of whether it exited from a box earlier than the median latency across the two groups, 309.5 s) on successive assays. We assessed

repeatability independently between assays 1 and 2 (for the first and second groups) and between assays 2 and 3 (for the first group only). We used standard binomial tests to determine whether observed repeatability was statistically significant.

We used a binomial generalized linear model with a logit link function to assess whether age or weight was predictive of individual boldness (the number of tests in which the individual exhibited 'bold' behaviour), with data pooled from both groups.

We also tested the repeatability between assays using a rank ordering of 'boldness'. We ordered individuals according to their escape latency times for each assay and tested the repeatability via Spearman rank correlation tests using these ranks. We also used the ordinal rank instead of the binary boldness and re-ran all the following analyses. All the model codes and results can be found in the electronic supplementary material.

Individual flight characteristics. In experiment 1, GPS tracks were first analysed in MATLAB, after converting raw positional data from degrees to metres using a Universal Transverse Mercator grid. We then extracted three measures from each solo flight's GPS data: speed, route efficiency and route fidelity. Speed was determined by the distance flown to reach home divided by the total time taken. Route efficiency was calculated by dividing the direct straight-line distance from the release point to home by the actual distance flown. Shorter routes therefore corresponded to higher efficiency values (approaching the maximum of 1). Route fidelity was measured as the mean nearest-neighbour distance between a focal track and the previous track. For each point on the focal track, the distance to the closest point on the previous track was measured, and the mean of these distances was calculated. Lower mean nearest-neighbour distances therefore corresponded to higher fidelity. Both here and in the subsequent leadership hierarchy analysis, we excluded segments of track within a 200 m radius of the release site and the loft. For each of our path characteristics, we used linear mixed-effect models to test for a fixed effect of either personality type (bold or shy), an interaction between personality type and release number, or both, controlling for bird ID as a random effect and a release number, weight and age as fixed effects. We used stepwise model reduction by elimination of non-significant effects to determine an optimal set of predictor variates in each case, sequentially removing the predictor or interaction with the greatest p -value and refitting the model until all remaining predictors were significant ($p < 0.05$). p -values were calculated by likelihood ratio tests (Wilks theorem, [39]) between a model including or removing the relevant predictor. We transformed efficiency and fidelity measures to obtain a linear relationship with release number. The details of these procedures and the results can be found in the electronic supplementary material.

Hierarchical leadership rank. In Experiments 2, 3 and 4, after converting raw data to metres as described above, pairwise leader-follower relationships, and overall hierarchical ranks derived from these, were determined by established statistical methods using delayed directional correlations of the recorded flight paths (see [29] for details). In short, we measured leadership by quantifying how often and how soon a bird was followed by others in the flock whenever it changed its flight direction. While pigeon-borne GPS devices record positional fixes with deviations of 0.00 ± 0.34 m (mean \pm s.d.; see [31]), they are highly accurate in recording directional changes and hence suitable for calculating leadership hierarchical positions based on correlations of movements [29,30]. Once we had obtained a leadership hierarchical rank for each bird, we analysed the effect of personality type on hierarchical rank, via ordinal (rank) regression models. We used a standard ordinal regression model, the cumulative link mixed model (CLMM). This is a generalized linear mixed effects model where the ordinal output variable is assumed to be generated from a logistic transform of a latent linear function of the predictors: the final output ranking is determined by the value of this latent function relative to a set of

ordered thresholds which specify the possible ranks (these thresholds being fitted parameters of the model). We used hierarchical rank as the ordinal dependent variable, personality type, weight, age and speed in solo flight (in Experiments 2 and 3), as well as interactions of these variables with release number, as independent fixed effects. Bird identity and group identity were included as random effects. As with our models of individual flight characteristics (see above), we used stepwise model reduction via sequential removal of non-significant effects to determine the optimal predictors of hierarchical rank in each experiment (see the electronic supplementary material for details). P -values for each effect or interaction were determined by likelihood ratio tests as above. All the results can be found in the electronic supplementary material.

In Experiment 4, seven flights in which more than five birds landed after less than 2 min were excluded. Owing to GPS device failure, we did not obtain any track data from two, six and two flights in Experiments 2, 3 and 4, respectively. Furthermore, we excluded the directional correlation delay times of pairs if their directional correlation values were below 0.5, indicating that the movements of birds in those pairs were not highly correlated [29]. If by filtering out such data, the majority of individual flight data in a flock (greater than 5, 4 and 7 birds for Experiments 2–4) was removed—i.e. birds did not fly as a coordinated flock—we excluded the entire flock flight from further analyses. This occurred in one, seven and four flock flights from Experiments 2, 3 and 4, respectively.

All statistical procedures were implemented in R (v.3.2.1). Data are available in the electronic supplementary material.

3. Results

(a) Pigeons have consistent personality

Individual personality was robustly repeatable. The number of birds exhibiting the same personality measure between assays 1 and 2 was 34 out of 45 ($p < 0.001$, binomial test for $p = 0.5$) for the first group. For the second group, this was 42 out of 50 ($p < 0.001$, binomial test for $p = 0.5$) both between assays 1 and 2 and between assays 2 and 3. Thirty-seven of 50 birds retained the same personality across all three assays ($p < 0.001$, binomial test for $p = 0.25$). One individual in the second group was not recorded in the second behavioural assay because it escaped from the box prior to the start of the trial. The Spearman rank correlation tests show the same patterns ($p < 0.001$ for all the repeatability tests; see the electronic supplementary material).

Neither weight ($p = 0.20$) nor age ($p = 0.09$) had a significant impact on the probability of a bold or shy response when pooling the data from both groups. When we analysed the two groups separately, we found no effect of age ($p = 0.44$) in the first group, nor of age ($p = 0.11$) or weight ($p = 0.97$) in the second group. However, we did find a significant negative effect of weight on boldness in the first group ($p = 0.007$). See electronic supplementary material for details of these effects.

(b) Bold individuals fly faster than shy ones during solo homing flights, but do not differ in route efficiency or fidelity

During solo flights, bold birds had significantly higher speed than shy ones ($p = 0.02$; figure 2*a*). The route efficiency and route fidelity were, on the other hand, not statistically different for bold and shy birds ($p = 0.05$ and 0.84 , respectively; figure 2*b,c*). The linear mixed models with stepwise model

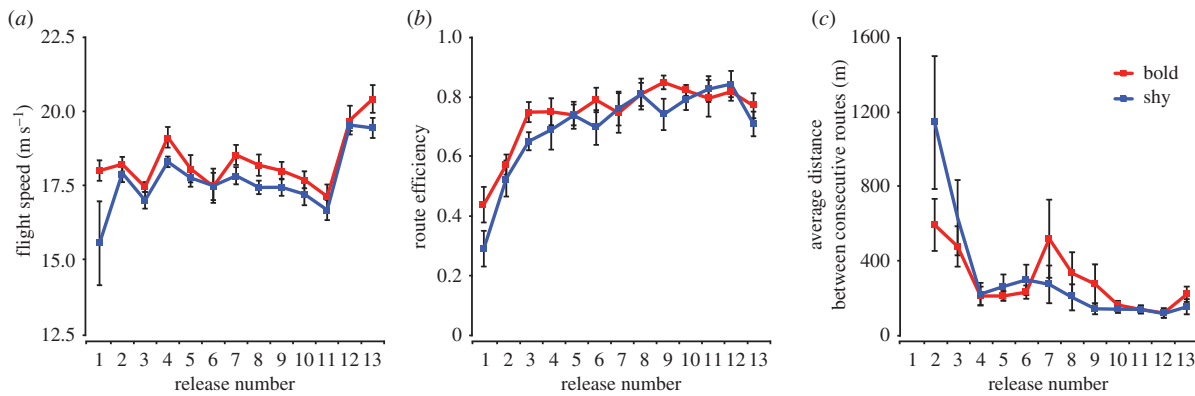


Figure 2. Flight characteristics of bold and shy homing pigeons over 13 consecutive solo flights. (a) Flight speed (distance flown to reach home divided by total time taken), (b) route efficiency (direct straight-line distance from the release point to home divided by distance flown; higher efficiency values mean shorter routes) and (c) route fidelity (mean nearest-neighbour distance between a focal track and the previous track; lower values mean higher fidelity).

reduction showed that all effects were non-significant for all the models, except release number ($p < 0.01$ for all), meaning that speed, efficiency and route fidelity increased the more the birds were released. See electronic supplementary material for details of the models and results.

(c) Bold birds occupy higher ranks in the leadership hierarchy than shy birds during homing flights from familiar and unfamiliar sites

The proportion of times that bold or shy birds occupied each rank in the leadership hierarchy, from 8 or 7 (lowest) to 1 (highest), are shown across all homing flights from familiar and unfamiliar sites in figure 3*a,b*. In both cases, bold birds disproportionately occupied higher ranks, while low ranks tended to be occupied by shy birds. In Experiment 2 (familiar site), there was a gradual decline in the proportion of times each rank was occupied by a bold bird, from highest to lowest, while in Experiment 3 (unfamiliar site) this change appeared more abrupt, with a distinct switch between ranks 3 and 4. However, it is impossible to ascribe this either to treatment (site familiarity) or to site-specific effects without additional experiments varying familiarity at the same release site (and ideally across multiple release sites). The CLMM analysis showed that bold birds were significantly more likely to occupy higher ranks in the leadership hierarchy than shy birds at both familiar and unfamiliar sites ($p < 0.01$ for both).

All other effects were not significant (electronic supplementary material), except for speed during solo flights ($p < 0.01$) in Experiment 3 (unfamiliar site), suggesting that faster birds were more likely to occupy higher leadership ranks. Additional analysis of our data using a Pearson correlation confirmed this previous finding [33] (electronic supplementary material, figure S1).

(d) Bold individuals occupy higher ranks in the leadership hierarchy than shy birds during free flights around lofts

The proportion of bold or shy birds occupying each position in the leadership hierarchy is shown across all free flights around the lofts in figure 3*c*. Similar to the results of the homing flights, higher ranks in the leadership hierarchy

were more frequently occupied by bold birds and low ranks were more often occupied by shy birds. In this experiment, the changes in personality across ranks showed a gradual change, as in Experiment 2, without the apparent sharp transition seen in Experiment 3. The effect of boldness on leadership hierarchy position was confirmed by CLMM analysis, with personality type identified as a significant factor in predicting leadership rank ($p < 0.01$). Again, none of the other effects were significant factors in predicting rank (see the electronic supplementary material).

4. Discussion

In this study, we investigated the relationship between personality and individual influence on collective movement in homing pigeons. Past studies investigating this relationship typically focused on the single most influential member of a group, despite the fact that many animal groups, including homing pigeons [29], have distributed leadership, meaning that more than one individual can influence collective movement [25]. Our results showed, for the first time, that bold individuals were more likely to occupy not only the highest rank but also the subsequent upper ranks in leadership hierarchies. This trend was observed irrespective of navigational context; the same pattern was detected during free flights around the lofts as in homing flights. Our data of solo homing flights further showed that bold birds flew significantly faster than shy ones, consistent with the recent finding that leaders tend to fly faster during solo flights than followers [33]. Another recent study showed that bold pigeons also have higher route solo efficiency than shy pigeons from novel sites (i.e. during their first release) [40]. Our solo data did not show this pattern for the first release (Mann–Whitney U -test: $W = 86$, $p = 0.09$), nor across 13 subsequent releases ($p = 0.052$). However, because these probability values were just marginally above the significance level ($\alpha = 0.05$), our results should be interpreted with caution. In pigeon flocks, birds contribute to group movement to differing extents: input from birds who occupy higher ranks in the leadership hierarchy carries, by definition, more influence (see [29] for details). Thus, our results indicate that bold birds have more influence on the direction of the flock's trajectory than shy birds, and they address intriguing

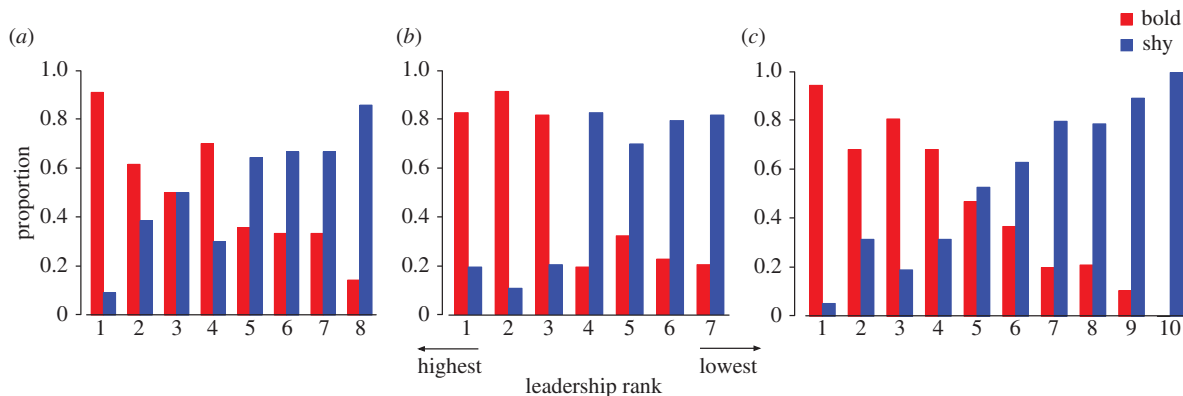


Figure 3. Proportion of times bold and shy homing pigeons were observed for each rank in the leadership hierarchy, across all flights. (a) Homing flights from a familiar site, (b) homing flights from an unfamiliar site and (c) free flights around the lofts. The group sizes were different for (a) and (b), and thus the lower ranks were not occupied in small groups (see the main text for details of group sizes).

questions about the consequences of individual variation on collective animal movement.

To the best of our knowledge, this is the first study showing that bold individuals tend to occupy not only the highest leadership rank but also the subsequent upper positions in a leadership hierarchy, and that this effect is robust across three different contexts (figure 3). The exact relationship between leadership rank and personality appears somewhat different across the three group-flight experiments in our study: some groups exhibited a gradual change in the proportion of bold birds occupying ranks from the highest to the lowest positions (figure 3*a,c*), while others showed a marked transition between the upper and lower halves of the hierarchy (figure 3*b*). Because there are other differences besides context across these experiments, such as group members, group sizes and release sites, we were not able to test whether the differences in the personality–leadership relationship apparent in figure 3 are the result of context or other factors. Future research is required to test if and how personality interacts with context (such as site familiarity) to influence collective organization in free-flying and navigating bird groups.

How do bold pigeons become leaders? Our data show that bold individuals tend to fly fast—they may thus end up in positions at the front of the flock where they then incidentally become leaders, as a recent study suggests [33]. Alternatively, it has been shown that bold individuals tend to pay less attention to social information than shy ones [41,42], so if this means that bold pigeons are less likely to follow others than shy ones then, by definition, they will emerge as leaders in our analyses.

A recent study showed that bold pigeons (measured as those that leave a confined space sooner) are less likely to be predated by raptors than shy ones [43], while it has been demonstrated that leaders have a higher vulnerability to predation in fish shoals [44]. Besides the fact that pigeon leaders may not always be at the frontal position [7,25,45,46], there are at least three other possible reasons for this inconsistency with the results from fish. First, bold birds may have other associated characteristics that help them avoid predation attacks. For example, our results suggested that bold pigeons are, on average, faster individual fliers, so leaders among birds may be better at escaping from predators than followers. In fact, a recent study has shown that bold pigeons

who demonstrated a lack of neophobia tend to develop more efficient routes and thus fly home faster during solo homing flights than shy birds who are neophobic [40]. Secondly, raptor attack strategies may be different from those used by aquatic predators. For example, it has been suggested that raptors' initial strikes are aimed at splitting up the flock to isolate individuals that can be then chased [1]. In this case, it may not necessarily be the case that the front position is riskier than others, as would possibly be the case in fish shoals. Thirdly, personality may not be consistent across different contexts [47,48]. For example, pigeons who are more willing to take risks and thus are categorized as 'bold' in a personality test conducted on the ground may not act as bold individuals in the air. In this case, bold pigeons would not necessarily have higher vulnerability to predation than shy ones when flying.

Finally, it is worth noting that studies of animal personality have recently come under criticism [49,50]. Two main issues have been raised. First, the field of animal personality research was originally developed to investigate correlations between the expression of different behaviours (also known as 'behavioural syndromes') and why and how these correlations evolve and are maintained [13]. Nonetheless, personality is now increasingly used to describe variation along a single behavioural parameter. Indeed, our study too measured only exploratory behaviour and categorized individuals into 'bold' and 'shy' personality types accordingly. The argument can, therefore, be made that our study, along with many others, is not technically measuring personality [49]. Second, because animal personality types and their respective measurement are not clearly defined, the same terms, for example 'boldness' and 'shyness', can and have been used for different behavioural manifestations [50]. These problems can be extrapolated to studies that investigate the relationship between personality and collective behaviour. For example, 'boldness' is measured in terms of social behaviour (e.g. how much individuals stay close to others; bold individuals are those that who pay little attention to others) in some studies (e.g. [18]), while in other studies it is measured by testing individual exploratory behaviour (e.g. [16]). These behaviours may not necessarily correspond to the same underlying trait, and thus, comparisons of these studies for extracting general principles of the relationship between leadership and boldness could be meaningless.

Nonetheless, with more standardized behavioural assays and greater clarity in terminology, these problems could be overcome [50,51].

Heterogeneity of group members can be important to facilitate effective collective decisions, as previous studies have demonstrated [1,52,53], but it is not yet clear exactly what the adaptive value of either boldness or leadership is in pigeon groups for the individual, or to what extent frequency dependence maintains a particular balance of personality types. For example, does a heterogeneous group (i.e. a group composed of both bold and shy birds) perform better than a homogeneous group [53]? Furthermore, is personality flexible under certain circumstances [54], such as being contingent on the personality types of other current group members [18]? If so, in a homogeneous group, do some group members change their personality types over time in a way that leads to the emergence of a heterogeneous group? What cues do they use to initiate such changes and do they track the performance of the group to inform their 'choice' of personality type? Since both individual personality and group performance are easily quantifiable in pigeon

flocks, future empirical data from this species have the potential to shed important light on such questions, and, more broadly, on burgeoning discussions about the evolution of personality, or individual variation, in animal groups [13,47,49,54,55].

Ethics. The protocols used in this paper were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. T.S. and D.B. designed the experiments. T.S., K.N.W., T.H. and T.W. performed the experiments. R.P.M., T.S. and D.B. designed the analysis of data. R.P.M. and T.S. performed the analysis of data. T.S., D.B. and R.P.M. wrote the paper.

Competing interests. We have no competing interests.

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